14. The Embryonic Development of the Porbeagle Shark, *Lamna cornubica*. By E. W. Shann, B.Sc., F.Z.S., Biology Master at Oundle School.

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(Text-figures 1, 2.)

Contents.

I. *Recapitulation.*

In 1910 I investigated the anatomy of the advanced embryonic stage of *Lamna cornubica*. My results were published in the Twenty-eighth Annual Report of the Fishery Board for Scotland. Simultaneously with this publication there appeared a much fuller account of the same subject, profusely illustrated, by Lohberger (4). As this author placed an entirely new interpretation upon the anatomy of the alimentary canal, as well as upon the mode of embryonic nutrition, I was desirous of repeating my investigations; I accordingly asked Dr. Williamson of the Scottish Fishery Board, who had supplied my original material, if ever he obtained more embryos of *Lamna* to give me the opportunity of dissecting them. Cases of the capture of *Lamna* embryos are few and far between, and it was not until 1922 that Dr. Williamson was able to comply with my request. In February of this year a female landed at Aberdeen was found to contain four embryos, each measuring about 35 cm. in total length. These embryos, together with the entire oviducts and ovaries of the mother, were placed at my disposal; for which I take this opportunity of thanking Dr. Williamson. One of these embryos was a male, which is of interest as being the first recorded case of the capture of a male embryo of *Lamna*.

As the result of my investigation of the latest material, I am able to confirm Lohberger's observations almost in their entirety; and this despite a strong preconceived scepticism regarding the possibility of his view of the nutritive process, a scepticism which was shared by all the zoologists with whom I had discussed the subject. Briefly, the facts regarding the development of the embryo are as follows:—

The original yolk-sac is absorbed at a very early period, when the embryo measures about 6 cm. Thenceforward the cardiac portion of the stomach becomes filled with semi-solid matter, which process distends the abdominal wall of the body to an incredible extent. The yolk-stomach so formed was erroneously described by previous writers (including myself) as a yolk-sac. The semi-solid matter is derived from the ovary of the mother and is actually swallowed by the embryo in the uterus. Feeding continues in this manner for a long time, certainly for more than a year, during which time the yolk-stomach continues to *increase* in size (unlike a yolk-sac) until it assumes gigantic proportions. It will be shown that there is a regular increase in the bulk of the yolk-stomach from the embryo of 35 cm. to that of 55 cm. Embryos have been found in the uterus measuring as much as 75 cm. (Pennant, **5**); unfortunately, no record is available of the measurements of the paunch, though it is said to be very large.

The smallest free-living specimens of *Lamna* measure 82 cm. (Day) and 87 cm. (Williamson); these, however, have lost all trace of the yolk-stomach, and in external appearance possess in every detail the character of the adult. Birth presumably takes place when the young shark measures about 80 cm. But to what purpose is the great accumulation of food in the stomach put? Certainly it is not used in body-building, for the free-living young are only a few cm. longer than the paunched embryos. It seems possible that the accumulation of nutrient matter in the embryo is used for the expensive purpose of building the reproductive organs, and that the young at birth are already mature*.

Such a condition would be unique among chordate animals; but, indeed, the very mode of nutrition of the embryo is unique. Viviparity among Elasmobranch fishes is by no means uncommon, and three general methods of nutrition are in vogue: either the yolk-sac forms a pseudo-placental connection with the uterine wall; or the latter secretes a nutrient fluid which is absorbed by means of external gill-filaments; or, again, the uterine wall itself produces long secretile villæ which enter the alimentary canal of the embryo by way of the spiracles. From all these recognized methods of embryonic nutrition the condition in *Lamna* forms a fundamental departure; moreover, whereas in other forms the maternal nutriment is used up at once in body-building, here the vast majority of it accumulates in the stomach as a reserve store.

After consulting the "Zoological Record," as well as from conversations with several eminent ichthyologists, I believe that I am now in possession of all the outstanding facts at present known regarding the embryonic development of *Lamna cornubica*. I have attempted in the following pages to arrange these facts in

* At the same time Dr. Williamson, in a letter to me, says: "A female 3 ft. 6 in. long, in October, was immature. Further, a Porbeagle 6 ft. long, in December, appeared to be a male, but it had only a slight indication of the external male characteristics."

logical sequence, and to interpret them in the light of my recent observations.

II. *Record of Material.*

Table I. contains a record of the captures of all *Lamna* embryos known to me, and in addition of the smallest free-living specimens. It is apparent at the outset that from the time when the embryo has attained a length of 25 cm. down to the time when it is approaching readiness for birth (75 cm.), we have a fairly complete series of records. None of the embryos in this series, however, differs in any important developmental character from

Table I.

Index.	Authority.	Month of Capture.	Length (cm.).	Embryos. Number and Sex.	Embryos. Length (cm.).
A	Swenander.	Jan.	—	2 ?	5·5 6·0
B	Calderwood.	—	—	?	25·0
C	Collet.	Dec.	—	?	29·0
D	Collet.	Jan.	—	2 ?	29·5
E	Swenander.	—	—	4 ?	30·0
F	Shann.	Feb.	150	1 ♂, 3 ♀	35·0
G	Collet.	Feb.	256	4 ?	42·5
H	Lohberger.	—	—	2 ♀	4·28 5·53
J	Shann.	Mar.	—	1 ? ♂	54·4
K	Shann.	—	150	4 ♀	45·4 60·5
L	Shann.	June ?	—	2 ?	47·5
M	Pennant.	—	—	?	70·0 75·0
N	Day.	—	82	(Smallest recorded free-living young.)	
O	Williamson.	Nov.	87		

the others; the period which they represent, in other words, is mainly characterized by growth in bulk. The only record of an earlier phase is that of Swenander (7), who states that the stalk of the original yolk-sac was present as a mere shred in embryos 5·5–6·0 cm. long.

From the fact that the smallest known embryos (A) were obtained in January, and that they measured not more than 6 cm., it may be inferred that fertilization takes place towards the end of the year. In December and January again we find embryos measuring 29·0 and 29·5 cm. (C, D); these have presumably been in the uterus for just over a year, since it is incredible that they are of the same age as the minute specimens noted above. Allowing for the incompleteness of the record, subsequent measurements bear out this supposition remarkably well. In February the embryos may measure from 35 to 42 cm., while at the end of March we find one measuring 54 cm. The last named is, according to our supposition, well on in the second year of intra-uterine development. The figures obtained for the months of December to March are sufficiently consecutive to rule out the supposition that they represent the lapse of a second year; in which case we may suppose that the rate of growth during this period is more rapid than during the first year, namely, about 8 cm. per month. This estimate of the rate of growth of the embryos during their second year, however, must be treated with caution; for an embryo (L) said to have been captured in June only measured 47·5 cm., which would reduce our hypothetical rate of growth to about 4 cm. per month. The rate of growth during this period is probably liable to variation; indeed, we find differences in length of 12 to 15 cm. between embryos in the same uterus (H, K). On the whole it seems reasonable to infer that the average rate of growth during the second year of intra-uterine development is 5 to 6 cm. per month.

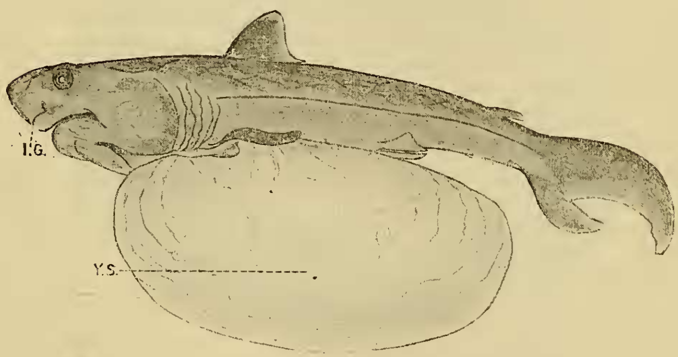
Dates of the capture of the larger embryos (M) are unfortunately lacking; but if growth continues at the rate indicated, we may suppose that they were captured about July and were then about 21 months old. This supposition, when taken with the observed fact that a free-living young specimen (O) was captured in November, seems to indicate that birth may take place in September or October, *i.e.*, approximately two years from conception. In what state the young are born is a matter of conjecture. The Table shows conclusively that the young at birth are not much longer than the largest intra-uterine specimens; moreover, they are approaching maturity, if not already mature. If the young are born with the yolk-stomach still distended it seems unlikely that in their unwieldy condition they could have evaded capture hitherto. Hence the suggestion offered above, namely, that the yolk store is used in building up the reproductive system. It is extraordinarily difficult to believe that the huge paunch is lost in the course of a few months without any apparent effect upon the growth of the young fish.

III. *External Features.*

The external features of the advanced embryo are amply illustrated in two earlier papers (Lohberger, 4, and Shann, 6). In order to save trouble in reference to other works, and at the same time to render the descriptions in this paper more readily intelligible, my drawing of an embryo measuring 454 mm. is reproduced in text-fig. 1. As there is no noteworthy difference in the external features between embryos of 350 to 605 mm., except in point of size, it is possible to make a general summary of the distinctive characters.

In its natural position the cylindrical body is curled around the massive paunch. The snout is extremely blunt and the whole head dorso-ventrally flattened, both of which characters are in strong contrast with the adult condition. There is an internasal groove. The pit beneath the chin shown in text-fig. 1 I now believe to be due to the shrinkage of tissues and not a normal character, for I have not observed it in any other specimen, nor does it appear in Lohberger's excellent photographs. The eyes are well developed. Teeth are prominent in both jaws, even in the smallest specimens examined by me (350 mm.), but

Text-figure 1.



Embryo of *Lamna*. × $\frac{3}{5}$.
I.G., internasal groove; Y.S., yolk-stomach (paunch).

they are devoid of the lateral cusps which are found on the teeth of the adult. Vestiges of spiracles are usually, but not invariably, present as minute pores situated midway between the eye and the first gill-slit; in no case yet examined do they communicate with the pharynx. Spiracles in the adult are either absent, or, if present, minute and functionless. The five pairs of large gill-slits are fully open, and the gills well developed (there are no traces of external gills). The lateral line is well marked. The lateral keels, so characteristic of the adult, in the caudal region are prominent, as is the notch in the back at the base of the caudal fin. The cloaca is open. The fins are fully developed and resemble closely those of the adult, excepting the caudal, whose dorsal and ventral lobes have not yet expanded so that they present the chelate appearance seen in the figure (at the same time the notch on the inner border of the upper lobe is distinctly visible).

The ground-colour is slate-grey fading to cream underneath and upon the paunch. The skin in the younger examples (350 mm.) is perfectly smooth, but in slightly larger ones (430 to 450 mm.) there is a slight roughness due to the developing scales. The skin passes without interruption from trunk to paunch (*i.e.*, without the deep crease which the illustration seems to indicate).

Table II. shows the detailed measurements of a series of embryos. The outstanding feature of this Table is the clear

TABLE II.

(All measurements are in millimetres.)

Index (see Table I.)	F	G	H	K	H	K
Length	350	425	428	454	553	605
Yolk-stomach { long axis	105	185	149	200	211	—
Yolk-stomach { short axis	52	—	95	135	123	—
Diameter of Eye	6	—	8	11	12	14
Tip of Tail to Yolk-stomach	—	—	211	—	267	—
Anterior of Cloaca to Root of Tail	95	—	—	100	—	125
Snout to 1st Dorsal Fin	125	—	131	166	178	220
1st Dorsal to 2nd Dorsal Fin	107	—	123	159	178	203
Pectoral to Pelvic Fin	90	—	97	120	131	—
Pelvic to Anal Fin	55	—	53	—	65	—
1st Dorsal Fin { base	25	—	25	44	43	57
1st Dorsal Fin { height	17	—	21	30	32	52
Pectoral Fin { base	20	—	21	26	30	40
Pectoral Fin { length	36	47	35	67	54	85
Pelvic Fin { base (transverse)	10	—	10	11	16	21
Pelvic Fin { length	20	—	22	29	29	35
Caudal Fin (outer rim) { upper lobe	115	121	115	145	147	168
Caudal Fin (outer rim) { lower lobe	45	54	54	75	82	85

demonstration that the paunch (due to the presence of the yolk-stomach) increases in bulk as the fish grows in size; we are thus forced to conclude that growth at this stage is not due to the use of reserve material, but to some external cause. The other measurements, apart from a few discrepancies (accountable either to normal variation or to individual methods on the part of different observers), give a very fair representation of normal growth.

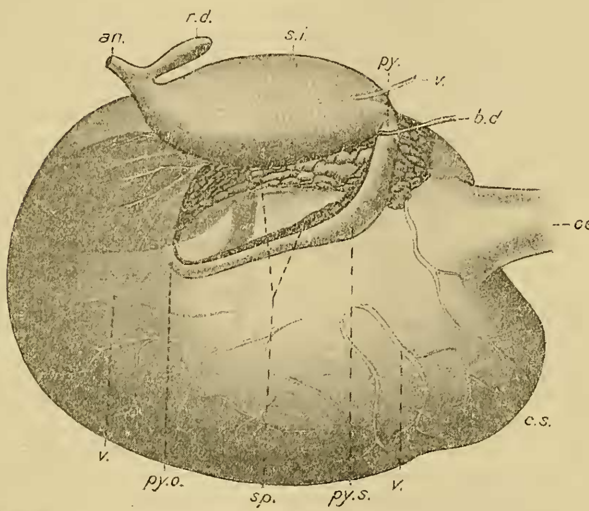
In the male specimen of 350 mm. the claspers of the pelvic fins are manifest even to a casual glance. The fins themselves showed the same measurements as those of the female twin (F).

IV. *Internal Structure.*

A full account of the internal structure of *Lamna* embryos can be obtained by reference to Lohberger (4) and Shann (6); thus it will be necessary here to give only a summary of the outstanding features of the alimentary system, together with certain corrigenda of previous statements. Text-fig. 2 is reproduced from Lohberger to illustrate my description of the alimentary system.

On dissection the outer skin in the abdominal region is found

Text-figure 2.



Alimentary canal of *Lamna* embryo (after Lohberger).

an., anus; *b.d.*, bile-duct; *c.s.*, cardiac portion of stomach ("yolk-stomach"); *oe.*, œsophagus; *py.*, pylorus; *py.o.*, origin of pyloric portion; *py.s.*, pyloric portion of stomach; *r.d.*, rectal diverticulum; *s.i.*, spiral intestine; *sp.*, spleen; *v.*, blood-vessels.

to be underlain by a thin layer of muscle, which is continuous with the lateral muscle of the trunk. The cavity within is a normal cœlom. The greater part of the cœlom is occupied by the swollen cardiac portion of the stomach, which in an embryo of 350 mm. had a volume of 150 c.c.; it is this organ, in fact, which causes the great ventral distension of the body-wall alluded to above as the "paunch." The wall of the cardiac stomach is richly supplied with blood-vessels. (The statement in my previous paper that the yolk "found its way into every interstice of the body-cavity, investing completely the abdominal organs" is, of course, erroneous; it arose through my having been content to dissect a specimen whose stomach had already been punctured.) Anteriorly the cardiac stomach tapers somewhat abruptly to the wide opening of the œsophagus. The latter organ is thick-walled and its lumen is longitudinally ridged; it communicates freely with the pharynx. Leaving the cardiac stomach in the region of the posterior third and slightly on the right side a narrow, but very muscular, tube runs forwards to enter the anterior end of the spiral intestine close to the point where the œsophagus debouches into the stomach. This tube is undoubtedly the pyloric portion of the stomach; it opens by a minute tunnel-like aperture into the cardiac portion, in whose wall it is embedded for some distance. The lumen, though minute, is nevertheless continuous from the cardiac portion to the spiral intestine. The latter organ is fully developed and passes posteriorly into the short rectum, which bears the characteristic dorsal diverticulum. The spleen is well developed (this is the "lobed tissue" whose significance I was unable to determine in my former paper). The pancreas is smaller and does not appear in the illustration, since it is situated on the left side. The liver is of large size and typical shape; it communicates by an apparently functional bile-duct with the apical intestine, entering it from the ventral aspect close to the pyloric opening.

In the youngest specimens examined by me (F) the muscles of the head presented a curious condition. The normal muscles (*e. g.*, constrictor, coraco-mandibularis, coraco-hyoideus, and coraco-branchiales) were recognizable, but instead of being composed of well-defined masses of compact muscle-fibres, the fibres were few in number and embedded in a mass of gelatinous non-cellular material. In older specimens this gelatinous matter gives place to true fibre; the process is correlated with considerable skrinkage in the relative girth of the head of the embryo.

There are five pairs of different branchial arteries, as figured and described by Lohberger. My previous description of six pairs I now consider to have been due to an error in dissection, for I have found only five pairs in the specimens examined since my first dissection was made.

V. *Physiology of Nutrition.*

The cardiac portion of the stomach (yolk-stomach) contains a mass of pale yellow-coloured pulp. The latter is finely granular as seen under the microscope: I failed, however, to find the dumb-bell-shaped granules described by Lohberger. The pulp is not uniform in consistency, for intermingled with it are irregular aggregations of skin-like matter, which Lohberger regards as portions of egg-membrane; indeed, he states that Swenander found two entire egg-capsules in the yolk-stomach of a 30 cm. specimen.

The uterine portion of the parental oviduct is thick-walled and highly vascular; its inner walls, moreover, are thrown into deep folds which have a glandular appearance. There is no evidence, however, that the uterine wall secretes a nutrient material. The uteri of specimens examined by Dr. Williamson contained, as he assures me, no substance apart from the embryos themselves. Swenander (7) found in the uterus of his specimen forty pieces of material, which proved to be groups of eggs surrounded by a common membrane. The portion of both oviducts immediately above the uterus in specimen F contained matter resembling the contents of the yolk-stomach, the lumen of the shell-gland was replete with it, and it was also present in the uppermost portions of the oviducts as far as their source; the skinny content, as might be expected, was not found above the level of the shell-gland. The ovaries themselves were large but contained no ripe ova; their contents much resembled in consistency the matrix in the yolk-stomach, but was darker in colour owing apparently to the accumulation of blood.

Not only did the matter in the yolk-stomach resemble that in all parts of the oviduct as regards physical properties, but a general chemical analysis conducted in the school laboratory revealed no outstanding difference in this respect.

Similar material was found in the mouth and œsophagus of each of the embryos of the F and H groups.

The only conclusion acceptable on this evidence is that nutrient material is derived from the ovary in the form of immature eggs or partially degenerate ovarian tissue—that this is taken up by the oviduct, is partially or completely covered with a thin membrane in the shell-gland, and is passed thence into the uterus, where it is swallowed by the embryos.

The contents of the spiral intestine are of a uniform semi-fluid consistency and of a greenish colour; they have, in fact, every appearance of having undergone the process of digestion. The rectum also contains greenish matter of a somewhat darker shade, and very slight compression of the trunk of the embryo (before dissection) causes this fæcal matter to exude from the cloaca.

These observations seem to show that food supplied by the ovary is taken into the alimentary system of the embryo through the mouth and digested in the manner characteristic of free-living animals. Owing to the sedentary nature of the embryo there is little wastage of tissue to repair; and, since the supply exceeds the demand, a vast surplus of potential food accumulates in the cardiac portion of the stomach. Whether all the waste products of digestion normally accumulate in the intestine of the embryo until birth, or whether a portion of them is voided into the maternal uterus requires investigation. If fæcal matter finds its way into the uterus it must be got rid of in some way. The passage of the uterus to the cloaca is short and wide; it is possible that water may enter and be expelled through this channel. Such a supposition offers an explanation of why no matter (whether nutritive or fæcal) is found as a rule in the uterus on capture. It also offers a solution to the problem of respiration; for, as has been shown, the gills are fully developed and apparently functional. The uterine wall is highly muscular, so that a potential mechanism for pumping water in and out of the uterus is present. Dr. Williamson, in a letter to me, says: "Mr. Ennson observed that the pregnant female dogfishes (piked dogs) when brought up in the trawl had the abdomen distended and sea-water poured out of the cloaca on to the deck."

Although the mode of embryonic nutrition described above, so far as I can ascertain, is unique among Elasmobranch fishes, certain observations by Gudger (3) on the Batoids of Beaufort, N.C., are worth consideration in this connection. Speaking of *Dasyatis say* Gudger remarks:—

"The young are found bathed in a substance of the color and consistence of rich yellow Jersey cream."

"The older embryos had the large intestine filled with a chlorine-yellow substance, evidently the milk-like food secreted by the villi and taken in probably through the spiracles." In the younger stages it is taken in by the long external gill-filaments.

"Notwithstanding the fact that the umbilical cord entered the alimentary tract at the junction of the small with the large intestine, and that the material in the anterior part of the large intestine was lighter in colour than in the middle and hinder regions, it is reasonably sure that it was not yolk." The material is described as "finely divided flocculent grading to large plate-like masses."

In this Ray and in *Pteroplatea maclura* when the uteri are gravid the ovaries are insignificant. The lumina of the ovaries were filled with "an abundant yolky material which probably came from the breaking down of some of the ova."

Gudger does not describe the contents of the upper parts of the oviducts: the question arises, did they contain any of the "yolky material" found in the ovaries? If not, how are we to account for the "large plate-like masses" which were found in the intestine: surely they do not come from a purely milky nutrition? Whether the nutrient matter is taken in through the spiracles (which in a Ray have sufficiently large openings) or through the mouth is a minor consideration; the important point is that food is actually swallowed and digested, according to Gudger, instead of being merely absorbed through gill-filaments. In the Rays, however, the supply does not exceed the demand, and, consequently, no yolk stomach is produced. The fact that in these Rays two batches of young are produced each season precludes the possibility of a protracted intra-uterine development such as occurs in *Lamna cornubica*.

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